New Jersey Teā (Ceanothus americanus).
Large toothed aspen (Populus grandidentata).
Carolina poplar (Populus eugenii).
Lombardy poplar (Populus nigra, var. italica).
Trembling aspen (Populus tremuloides).
Witch-hazel (Hamamelis virginiana).

The biological development of the individuals occurring on American ash, European ash, fringe tree, laurel leaved willow, large toothed aspen, and Lombardy poplar has been followed and found to agree closely throughout the life cycle with that of the lilac form.

In conclusion it may be said that the evidence certainly seems to justify an affirmative answer to the question, "Are there two species of the Oyster-shell Scale?"

LITERATURE CITED.

Cockerell, T. D. A. Miscellaneous Notes on Coccidae. Can. Ent., 1895, 27:259.
Frank, A. B. and **Kruger, F.** Schildlausbuch, 1900, 95.
Glenn, P. A. Forms of the Oyster-shell Scale in Illinois. Jour. Econ. Ent., April, 1920, 13:173-177.

A STUDY OF THE WING VENATION OF THE COLEOPTERA.*

By S. A. Graham.

The purpose of the modern taxonomist is not satisfied by the mere arbitrary naming of an insect. Taxonomy is more than that. If the worker in this field is true to the highest ideals of his profession he must continually strive to clear up some of the multitude of problems associated with the natural relationship of the organisms with which he is dealing, and to show this relationship in his classifications.

Unfortunately valuable phylogenetic characters are sometimes accidentally overlooked and remain in obscurity. It is not until we take advantage of all these available characters that we can hope to arrive at a true expression of phylogenetic relationship.

In the Coleoptera the characters to be found in the hind wings are undoubtedly of considerable value, but have been almost entirely neglected in taxonomic studies. This is

*Published with the approval of the Director as Paper No. 228 of the Journal Series of the Minnesota Agricultural Experiment Station.

perhaps partly due to the fact that these organs are hidden from view beneath the elytra and cannot be studied without relaxing dried specimens, and partly due to the fact that the homologies of the wing veins of this order have never been thoroughly worked out. It is the object of this paper to show in a preliminary way some of the neglected possibilities of these organs in the taxonomy of the group, and to show how the venation of the Coleoptera may be homologized with that of other orders. In this study a large series of wings, representing the most important families of the order, has been examined, but the work is still far from complete.

On examining a series of Coleopterous hind wings, several general outstanding features are apparent. First, that there is a distinct type of venation characteristic of the order. This is remarkably constant when the size of the group is considered. Second, there is considerable similarity between the venation of beetle wings and that of other insect orders, indicating the common origin of winged insects. Third, that within the order Coleoptera there are several types of modification which may have phylogenetic significance.

A study of the literature, however, fails to reveal any comprehensive investigations presenting conclusive evidence as to the homology of the wing veins of Coleoptera with that of other insect orders.

THE RELATION OF FOLDING TO VENATION.

One of the most striking features characterizing the wings of the Coleoptera is the fact that they are not only folded longitudinally, but also have at least one definite transverse fold. The advantage to the insect of this type of folding is obvious as it results not only in narrowing, but also in shortening of the wings when these appendages are folded against the body. This brings the wings under the elytra for protection. This protection is particularly essential to an insect of retiring habits living in places where an unprotected wing membrane would almost certainly be torn.

The fact that these folds or furrows necessarily follow the lines of least resistance between veins, usually running parallel with, and often very close to a vein, led Woodworth to associate them with the formation of veins. There is obviously some correlation between these two structures, but it seems to be more probable that folding was a modification coming after the development of wing veins and that the position of the folds was influenced greatly by the position of the veins. The folds naturally would follow along lines of least resistance, thus bringing about a mutual adjustment of position between folds and wing veins.

As a rule the folds lie parallel to veins, but if the venation becomes so modified that a fold must cross a vein the result is often a thinning if not an actual break in the vein at the point of crossing, similar to the bullæ so common in the Hymenoptera. The crossing of a vein by a fold is usually nearly at right angles in the order Coleoptera.

TRACHEATION AND VENATION.

In most orders of insects the tracheation of the pupal wing furnishes the key to the wing venation, but in the Coleoptera the tracheation is of little assistance. In this study the tracheation of only a few species has been examined, but in these there was considerable variation within a single species, (*Tribolium confusum*). Further study may show a correlation between these structures in the more primitive types, but for the present we may assume that the primitive position of the tracheæ is probably better indicated by the position of the wing veins which, in some groups of this order approach very closely the primitive hypothetical type of Comstock and Needham.

HYPOTHETICAL PRIMITIVE COLEOPTEROUS TYPE.

By the comparison of a large series of wings representing most of the families of the Coleoptera it has been possible to develop theoretically an hypothetical primitive type of venation for this order which does not differ greatly from the hypothetical primitive type of the class Hexopoda as proposed by Comstock and Needham. The Coleopterous type is characterized by a single branched Sc, a fusion of R_3 and R_4 at their tips, and by a similar fusion of R_5 and M_1. Also the first forks of R, M, and Cu are typically well toward the base of the wing. (Fig. 1).

Briefly, costa lies in the front margin. The next vein behind costa is the single branched sub-costa. Radius is five branched, the radial sector leaving R_1 near the base. R_2 turns forward to the front margin, while R_3 fuses with R_4 and R_5 fuses with M_1. The other veins do not depart from the hypothetical type of the Hexopoda in general; media being four branched, cubitus being two branched, and the three anals being present.

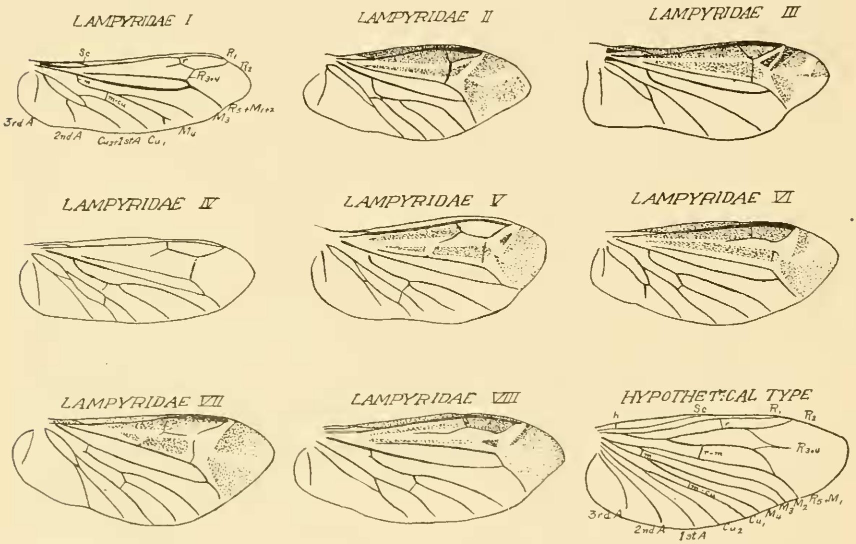

FIG. 1.

I. *Calopteron reticulatum* Fab.
II. *Podabrus tricostatus* Say.
III. *Chauliognathus pennsylvanicus* Fab.
IV. *Photinus pyralis* Linn.
V. *Photinus marginalis* Lec.
VI. *Eros aurora* Herbst.
VII. *Pterotus obscuripennis* Lec.
VIII. *Caenia dimidiata* Fab.
IX. Hypothetical Coleopterous Type.

COLEOPTEROUS WINGS IN GENERAL.

It is possible that costa is not always present, but whenever it occurs, it always lies in the front margin.

Sub-costa lies in the normal position and usually fuses with R_1.

Radius 1 lies just behind Sc and is always close to the front margins of the wing. In some species R_1 is so thickened as to almost obscure Sc.

The Radial sector leaves R_1 near the base of the wing and soon branches. R_2 turns forward to the margin, often fusing with R_1. R_3 turns backward and fuses with R_4. In the majority of Coleopterous wings R_3 and R_4 form a cross vein between R_2 and R_5, but the various stages leading up to this condition are found in species of several families, for example, Cerambycidæ, Chrysomelidæ, Bostrychidæ, Spondylidæ, etc. (See Fig. 3). In every wing examined, the radial sector is broken at the base and in many cases the basal part is entirely gone.

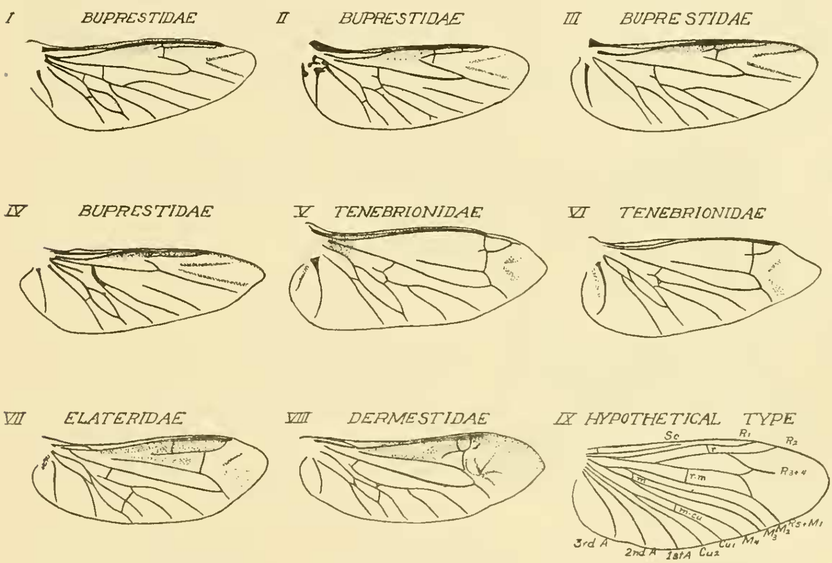

FIG. 2.

I. *Buprestis fasciata* Fab.
II. *Dicerca tenebrosa* Kby.
III. *Dicerca divaricata* Say.
IV. *Choleophora liberta* Germ.
V. *Upis cerambycoides* Linn.
VI. *Nyctobates pennsylvanicus* DeG.
VII. *Elateridae*
VIII. *Dermestes lardarius* Linn.
IX. Hypothetical Coleopterous Type.

Media is typically four branched, but in the Coleoptera M_1 and M_2 are always coalesced so that they appear as a single vein. The first fork of M is near the base. Usually the basal part of branch M_3 and M_4 is lost up to the medial cross vein so that the cross vein appears to be the base of that branch. The lost basal part is, however, often indicated by a spur or in a few cases may be present as in *Buprestis fasciata*. (Fig. 2-I).

Cubitus is always two branched, but these may be fused at the tip. Three anals are typically present and the 3 A is almost always separate from the other two. 1 A may either anastomose or coalesce with Cu and seldom appears as a separate vein for its entire length, while 2 A is usually fused with 1 A at least at the base.

The usual cross veins are found represented in the order, but it is unusual to find a wing in which they all occur. The humeral cross vein is usually either absent or obscured by the thickening of the veins in that region. Radial cross vein is almost always present. The Radio-medial cross vein is absent except in a single group of families of which the Carabidæ are typical. The medial cross vein and the medio-cubital cross veins are usually found normally.

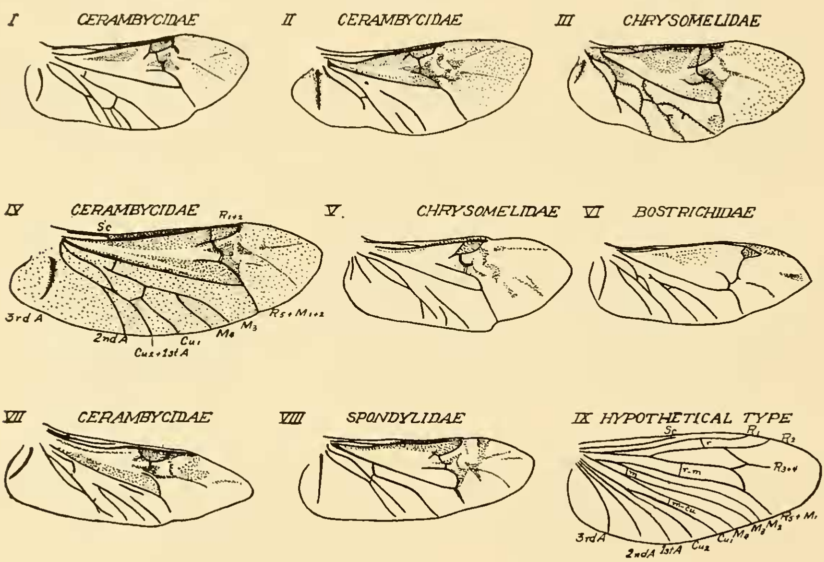

FIG. 3.

I. *Acaemops bivittatus* Say.
II. *Tetraopes femoratus* Lec.
III. *Chrysochus auratus* Fab.
IV. *Desmocerus palliatus* Forst.
V. *Donacia* sp?
VI. *Bostrychus bicornus* Web.
VII. *Monohomus confusor* Kby.
VIII. *Parandra brunnea* Fab.
IX. Hypothetical Coleopterous Type.

LINES OF MODIFICATION.

One of the most striking lines of modification is to be found in the fusion of tips of the veins in the apical area and a pushing back of the primary venation toward the base of the wing. The veins are replaced by secondary solid thickenings or calosities in the apical area which often resemble veins so closely that it is only by the study of a series of wings that their origin becomes clear. The presence of these secondary vein-like calosities has undoubtedly led to much confusion in studies of the wing venation of this order. In the plates these structures are indicated by stippling, while the true veins are represented by solid lines.

The pushing toward the base of the primary venation, as mentioned above, is apparent in the most primitive types of Coleopterous wings studied, but is much more striking with increased complexity of folding. The extreme of this modification is found in the Staphylinidæ, but a highly specialized condition is also apparent in other widely separated families such as the Scarabaeidæ, Silphidæ, Nitidulidæ, Ipidæ, and Curculionidæ. Thus it appears that this line of modification is correlated with the complexity of folding. Increased complexity of folding is made necessary in two ways. Either by a shortening of the elytra as in the Staphylinidæ or by shortening and thickening of the body, thus decreasing the elytral length as compared with the wing length as in the Scarabaeidæ.

Along with this migration of the primary venation toward the base of the wing and due also to increased complexity of folding, there occurs a reduction of veins. Also many veins become broken and branches become entirely separated from the veins of their origin.

PHYLOGENETIC SIGNIFICANCE.

It is apparent that the final determination of phylogenetic relationship cannot be based upon wing venation alone any more than it is possible to base such relationship upon tarsal, thoracic, or any other set of characters alone. The wings do, however, give some hints which will undoubtedly be of considerable value when correlated with other characters.

The first point which is brought out in this study is that the Lampyridæ, using that term in its broad sense, are characterized by a much simpler type of venation than any other group of the order. The venation of this family approaches very closely what was probably the primitive type. This, coupled with the fact that the Lampyridæ exhibit other primitive characters, such as soft wing-like elytra, soft integument, a larger number of abdominal segments than usual in this order, elongate body form, and long, many-jointed antennæ, would seem to justify the suggestion that this family may represent the most primitive of modern beetles. If this is true, it seems probable that the Coleoptera had its origin in a Lampyrid-like ancestral form.

On the other hand, the Carabidæ exhibit a distinct and rather a specialized type of venation which is characteristic of a group of families, including the Gyrinidæ, Dytiscidæ,

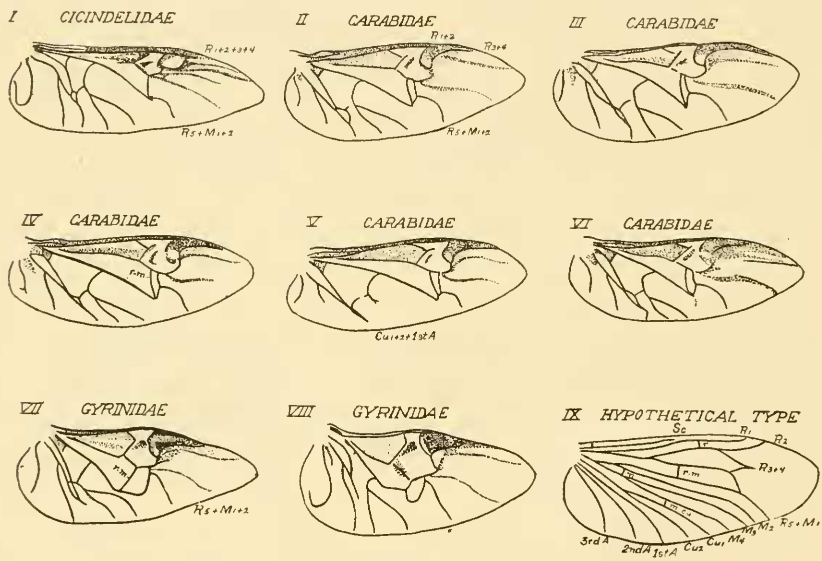

FIG. 4.

I. *Cicindela vulgaris* Say.
II. Carabidae.
III. *Harpalus caliginosa* Fab.
IV. Carabidae.
V. Carabidae.
VI. *Anisodactylus discoideus* Dej.
VII. *Gyrinus analis* Say.
VIII. *Dineutes assimilis* Aube.
IX. Hypothetical Coleopterous Type.

Cicindelidæ, and probably others. (Fig. 4). This group is characterized by the presence of cross veins r – m, by the persistence of the fused part of $R_3 + R_4$ which turns forward to the margin of the wing, and by the fact that the transverse fold cuts through branches R_{2+3} and $R_{,4}$ leaving these veins in the apical part of the wing.

The Cerambycidæ and Chrysomelidæ typify another group of families having similar venation. This type includes a large proportion of the families of Coleoptera, for example, Buprestidæ, Tenebrionidæ, Elateridæ, Bostrychidæ, Spondylidæ, Cistelidæ, Melandryidæ, Oedermeridæ, Pythidæ, Trogositidæ, Erotylidæ, Colydidæ, Mycetophagidæ, Mordellidæ, Meloidæ, and others.

This group is characterized by the fading out of the fused part of R_{3+4}, leaving a straight vein between R_2 and R_4. The

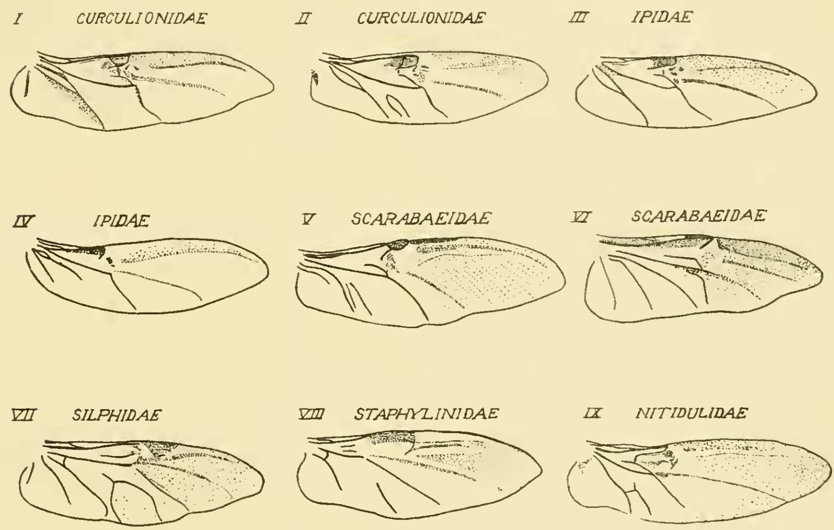

FIG. 5.

I. Curculionidae.
II. *Pissodes strobi* Peck.
III. *Hylobius* sp?
IV. *Ips* sp? (Ipidae).
V. *Bolbocerus lazarus* Fab.
VI. *Osmaderma eremicola* Kn.
VII. *Silpha inaequalis* Fab.
VIII. Staphylinidae.
IX. *Ips sanguinolentus* Oliv. (Nitidulidae).

various steps of this process are shown in species of Cerambycidæ, Chrysomelidæ, Spondylidæ, and Bostrychidæ. The transverse fold in this group cuts off the primary venation from the apical area of the wing.

We still have left a group of wings which have become so specialized that the venation gives very little hint of possible relationships and need not be discussed except to say that a number of widely separated families are represented. (Fig. 5).

SUMMARY.

1. A large series of hind wings, representing most of the important families of the Coleoptera, have been examined and the following conclusions seem justified:
2. The hypothetical primitive type of Coleopterous wing does not differ greatly from the Hypothetical type proposed by Comstock and Needham for the Hexapoda in general.
3. The hypothetical Coleopterous type is characterized by a fusion of R_3 with R_4 at the tip and by a similar fusion of R_5 and M_1.
4. The usual cross veins are typically present.
5. Modification of the venation goes hand in hand with an increase in the complexity of folding.
6. In general there are two types of modification:
   (a) A pushing back of the primary venation toward the base of the wing and the substitution of secondary thickenings in the apical area.
   (b) The reduction and breaking up of the veins.
7. The types of venation fall naturally into four groups.
   (a) Represented by the Lampyridæ which is the simplest type and may indicate the possibility of a Lampyrid-like ancestral form for the Coleoptera.
   (b) Represented by the Cerambycidæ and Chrysomelidæ in which R_3 and R_4 have become a simple cross vein between R_2 and R_5, and where the primary venation is cut off from the apical area.
   (c) Represented by the Carabidæ which is characterized by the persistence of the fused portion of R_3 and R_4, the presence of cross veins $r - m$, and the cutting of R_{2+3} and R_4 by the transverse fold.
   (d) A group of widely separated families where the venation is too highly specialized to show any relationship.